

## Long distance, directional migration on snow in a forest collembolan, *Hypogastrura socialis* (Uzel)

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*Hypogastrura socialis* is well known for its mass occurrence on snow during mild weather. This behaviour has been considered to have a migratory function, allowing the animals to identify suitable, snow-free patches below trees where reproduction can start early. Detailed studies in the present work on the migratory behaviour of single individuals and populations indicate directional movements over long distances, 200–300 m per day. Each individual repeatedly jumps in a certain direction and keeps a steady course on the snow surface. Before each jump, the animal rotates horizontally, probably using the sun for navigation. Individuals of the same population vary somewhat in jumping direction, but the whole population shows a main direction. The animals are able to navigate steadily also in shadow and after sunset, and a fixed direction can be kept through a mosaic of dense forest and open areas. Furthermore, an animal is able to avoid a dark obstacle (which might be a tree stem) by changing its course and to resume the original direction afterwards. This long-distance migration strategy on snow (including snow-covered ice) enables the species to cross habitats which would otherwise represent physical barriers in the landscape (e.g. rivers, wetlands and lakes).

### 1. Introduction

*Hypogastrura socialis* (Uzel) is a holarctic forest collembol, well known for its temporary mass occurrence on the snow (Latzel 1907, MacNamara 1919). Leinaas (1981a) showed that the species during favourable temperature conditions migrated vertically through the snow layers, and densities above 4000 ind. per m<sup>2</sup> could be achieved on the snow when surface air temperatures exceeded 0°C. During summer, he found the species highly aggregated in well-drained heaps of needle litter below certain spruce trees. Here moulting and egg-laying occurred synchronously in spring. The spring and summer behaviour was guided both by photoorientation and chemical communication (Leinaas 1983a, b). The winter activity was explained to have two functions: The location of early snow-free patches for new colonies, and the genetic mixing of populations.

In the present work, the migration behaviour of *H. socialis* on the snow surface was studied in detail, both on the individual level and for whole populations. Preliminary observations made by the author indicated that single individuals had a clear directional movement, and that whole

populations might migrate over considerable distances. High densities of the species could for instance be found on the snow cover or ice of rather large lakes.

### 2. Material and methods

The study was performed in a high altitude spruce (*Picea abies* (L.) Karst.) forest, about 800 m a.s.l., at Vegglijell, Numedal, Buskerud County (about 100 km W of Oslo). The landscape has varied topography, and the forest is interrupted by a mosaic of lakes, rivers and bogs. During the period 25–29 March 1991, sunny weather with air temperatures above 0°C and a moist snow surface initiated daily mass migrations of *H. socialis* on snow through the whole landscape studied (approximately 20 km<sup>2</sup>). Snow depth was approximately 1 m.

The following kinds of observations were performed:

- 1) Individual movement patterns on snow were mapped by marking each jumping point with a small hole in the snow and afterwards drawing up the migration

route. Tests showed that the approach of a person from behind did not change the direction of an individual's movement. Therefore, the observer was always behind the animal, but without posing shadow on it. Migration rates were also noted.

- 2) The main migration direction of selected populations were recorded by noting the direction of many individuals. Because each individual tended to keep a certain direction consistently, the record of one or two jumps was sufficient to indicate the individual's main direction. By observing at a distance of approximately 1 m, my presence did not influence the behaviour, even of animals jumping towards me.
- 3) Observations were performed to clarify whether navigation was possible in shadow and after sunset. The migration direction of certain populations were followed during the day, and also after a night period when the animals withdrew into the snow.
- 4) The effect of placing a dark obstacle in front of the animal was studied, to simulate the approaching of a tree stem.
- 5) The sun's position was noted during all observations. To study the possible use of the sun in their orientation, the sun's position was manipulated with a mirror.

### 3. Results

#### 3.1. Individual behaviour and migration pattern

Fig. 1A shows the individual routes for thirteen animals in a population which migrated from a forest edge onto the snow-covered ice of a 200 m broad lake. While each animal followed a consequent direction, there were individual differences in the directions. However, the whole population kept a main direction. With an air temperature at 2 m height of about 10°C and bright sunshine, the mean jumping length was 10 cm, and 8 jumps were performed per minute. This means that the 200 m broad lake could be crossed in four hours. There were approximately 1000 migrating animals per m<sup>2</sup>.

Before each jump, the collembol always performed a characteristic behaviour: On the spot it rotated the body 360° or less, just enough to bring the head in the correct direction. Then it jumped immediately. This would indicate an orientation in relation to the sun. Manipulation of the sun's position with a mirror confirmed this at a later occasion. Shadowing the sun and illuminating the animal from the opposite side initiated a 180° shift in migration direction. When the mirror was removed, the original direction was resumed. One animal was initiated to reverse its direction six times in this way.

Figs. 1B and C show individual migrations in two spruce forest sites during the next day, a few kilometers apart. It was still sunny, but with an air temperature at 2 m height of 4°C. In this somewhat colder weather, the mean jumping length was 8.7 cm, with 6 jumps per minute and a mean migration rate of 52 cm per minute (based on 68 jumps distributed on 9 animals). Sites B and C confirm the

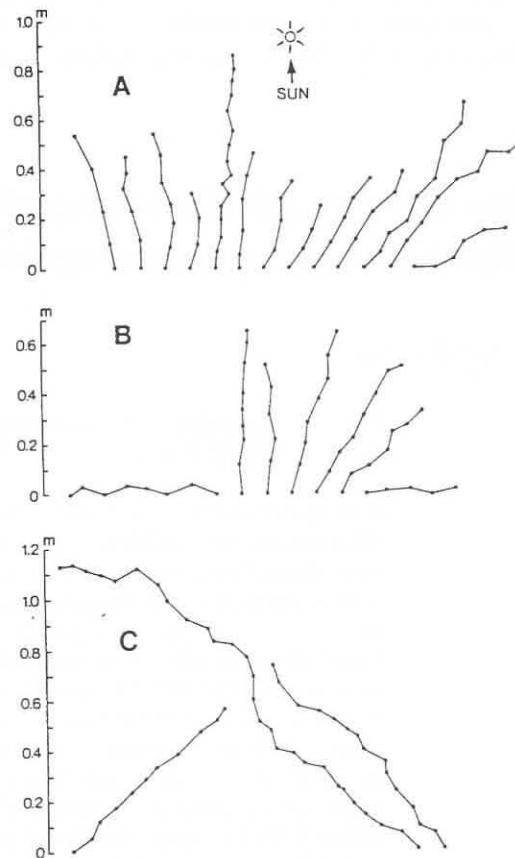


Fig. 1. Directional movements on snow in individual *Hypogastrura socialis* animals. Examples from three different populations (A, B and C). Dots indicate starting points for each jump. The animals moved upwards in the figure.

constant course of each individual, and the variation in directions between animals.

Since a consequent direction sooner or later would bring the animal in contact with obstacles like tree stems or stones, the effect of putting a dark object in front of the animal was studied. Figs. 2A and B illustrate how two animals changed their course when a dark spade (approximately 20 × 20 cm) was placed 30–40 cm in front of the animal (broad line indicates the spade and hatched area its shadow). Figs. 2C–E show that three animals which were followed further, resumed their original course after the obstacle had been passed by the sideway movement.

In Fig. 2F, the observer's body was 30–40 cm in front of the animal twice during the recorded migration route: first continuously between points 1 and 2, and then between points 3 and 4. The body with its shadow could indicate an obstacle. Both times, the animal reacted spontaneously by turning its course to the left. This new course was kept as long as the obstacle remained in front of the original

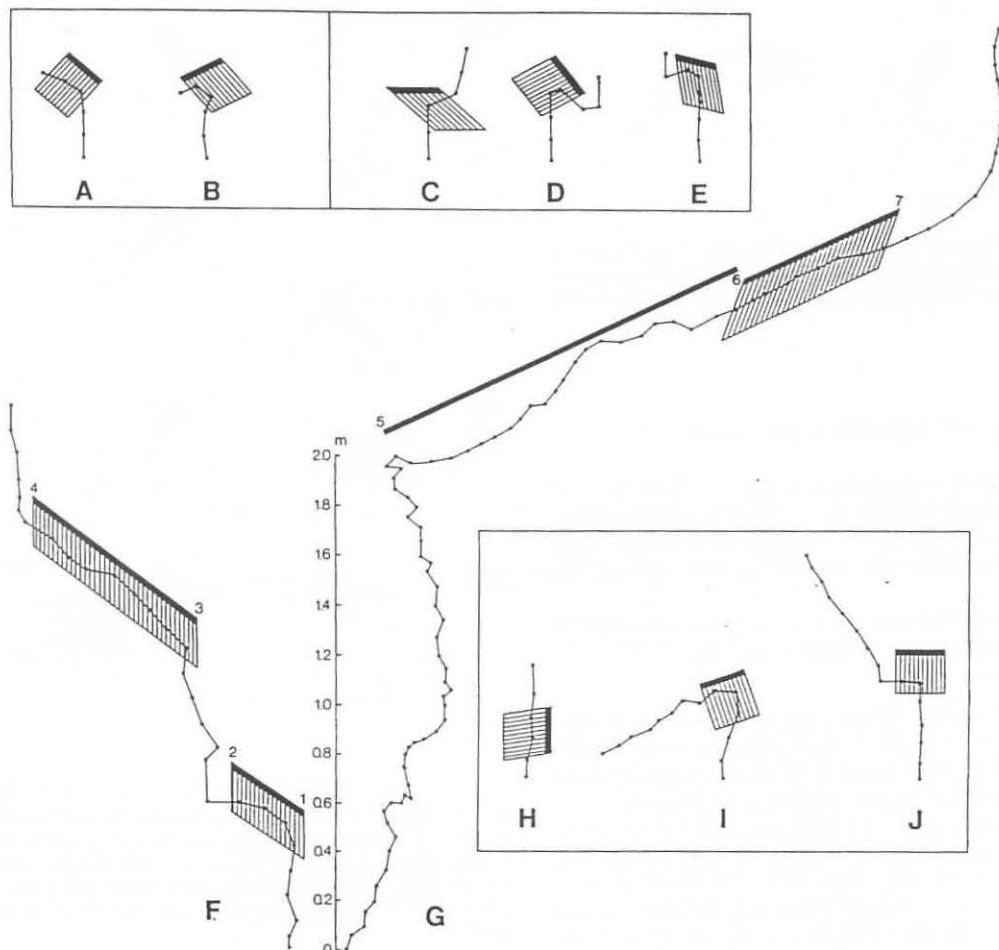


Fig. 2. Examples showing the ability to avoid a dark obstacle in the front of the animal's course. A thick line represents the obstacle, and hatched area indicates shadow. Each animal moved upwards in the figure. Further explanation in the text.

direction. However, both at points 2 and 4, where the obstacle was removed, the collembolan immediately returned to its original direction.

A similar experiment was performed with another animal after having recorded the natural migration over 2 m (Fig. 2G). As long as I continued to locate myself in front of the original direction, the animal followed a new direction to the right. This was independent of whether my body posed a shadow on the animal (points 6–7) or not (points 5–6). When I moved aside, the animal resumed its original direction.

Fig. 2H shows a collembolan freely passing through a shadow when no obstacle lies in the course. Figs. 2I and J illustrate two cases where the animal established a new course after having passed the obstacle, especially 2I. According to additional observations (not drawn), most animals remember their original course.

In Fig. 3, the migratory course of some collemboles approaching a dark tree stem is shown. The animals tended

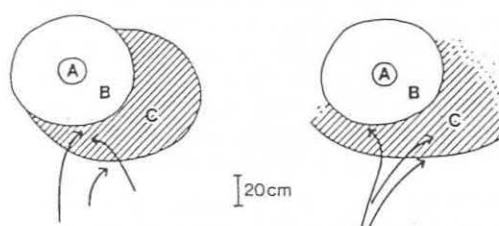


Fig. 3. Changes in the animal's route when approaching a tree. A = tree stem (spruce), B = funnel-shaped depression in snow around the stem, C = shadow. Lines with arrows show the routes of individual animals.

to change the direction in an avoiding movement. Due to a high density of jumping animals on the snow, specific individuals were difficult to trace over long distances.

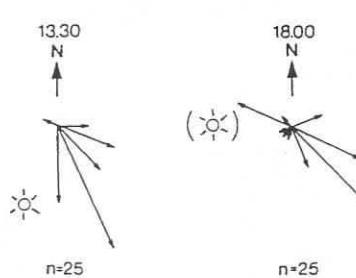


Fig. 4. Individual migration directions on the same locality at two different times of the day. The sun's position is indicated (sun in brackets means that observations were made after sunset).

### 3.2. Migratory behaviour of populations

A population crossing a small, open site kept the same main direction towards SE at 1330 p.m. (sunny weather, with 4°C at 2 m height) as at 1800 p.m. (just after sunset, temperature below zero and hardened snow surface) (Fig. 4).

Another population crossing a 20 m wide bog was studied during three succeeding days (Fig. 5). The main conclusions were:

- 1) During nearly 24 hours (left half of Fig. 5), the main direction was SW. Then the direction turned towards SE (right half). Whether this change might be due to the arrival of another population, is unknown.
- 2) Just after sunset 26.3 (1800 h) and 27.3 (1845 h), the animals continued to migrate, but hesitated more and often rotated several times before they decided to jump. Soon after, the moist snow cover hardened, and the animals rapidly withdrew into the pores of the snow to avoid low temperatures.
- 3) In both mornings, when migrations continued, (27.3 and 28.3 at 1100 h), the animals clearly "remembered" the direction from the evening before.
- 4) The effect of a dark period was studied by keeping eighteen animals in a plastic box for 4 hours deep in the snow. While their direction was originally SE, most animals moved NW after the dark period, i.e. a change of 180° (Fig. 5, lower right). During the dark period, they had changed their behaviour from moving to the left of the sun, to move to the right of it.

Observations on a population crossing a 15 m broad bog showed that the animals kept a rather steady direction, independent of changes in light and shadow (Fig. 6). Both before crossing the bog (A, in sunshine) and afterwards (D in shadow), the main direction was SW. Transporting animals across the bog, from A (sunshine) to B (shadow), did not significantly change their main direction. When shadow fell on the A area, animals proceeded to migrate into the open bog, although in a slightly more western direction (C). The animals are obviously able to migrate without a

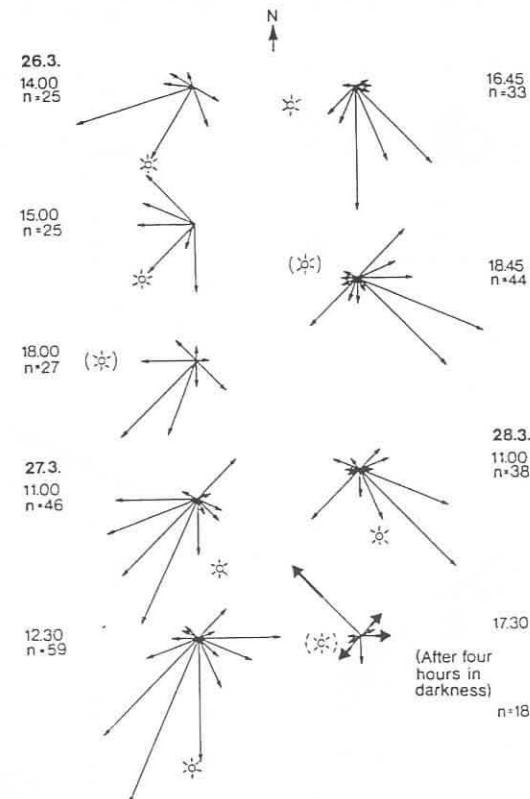


Fig. 5. Individual migration directions on the same locality during three succeeding days. The date, the time of the day, the number of animals observed, and the sun's position are indicated (sun in brackets means that observations were made after sunset). The last observation was made partly in sunshine (thin arrows), and partly after sunset (thick arrows).

visible sun, and both at C and D, the sun was below the local horizon. However, in the darkest site (D), the animals often rotated several times before jumping, needing more time to find the correct direction.

## 4. Discussion

### 4.1. Long-distance migration as a strategy

Winter migrations of *H. socialis* must be seen in relation to the species' extremely aggregated distribution during summer (Leinaas 1983c). The thick needle mats below certain spruce trees, which are selected for reproduction, represent both a patchy and temporary habitat. This favours, or demands, a high dispersal ability (MacArthur & Wilson 1967, Leinaas 1983c). A closely related species, *H. lapponica* (Axelson), which lives under the bark of specific birch trees, and thus also inhabits a patchy and

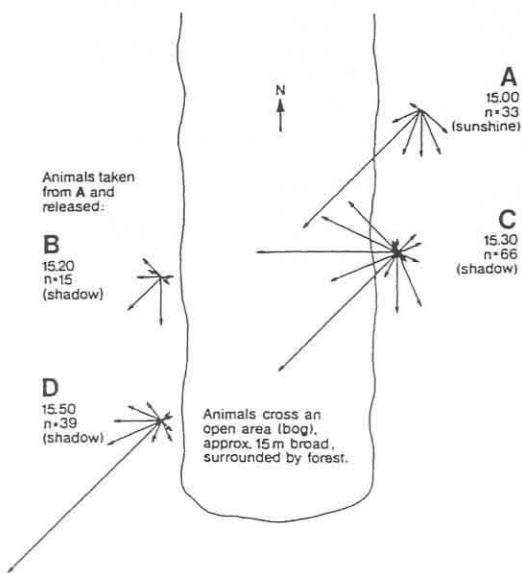


Fig. 6. Individual migration directions of animals crossing an open bog. Further explanation in the text.

temporary habitat, shows a similar adaptation to dispersal on snow, although less intense than *H. socialis*. According to Leinaas (1981b), animals are rarely found more than 30 m from the nearest tree.

The strategy of *H. laponica* seems to be a short-distance migration, long enough to reach another "isle", but not so long that it would bring the animals into unfavourable habitats. *H. socialis*, however, has an ability to cross inhospitable habitats, including mires and large, snow-covered lakes. Such a long-distance migration would demand a persevering jumping activity, an ability to keep a steady course over long distances, an ability to avoid obstacles underway, and an ability to terminate the migration in a favourable microsite. *H. socialis* seems to have developed these skills.

#### 4.2. Navigation ability and behaviour

The manipulation of light direction with a mirror showed that the animal consequently jumped at a certain angle relative to the visible sun. The obligatory horizontal rotation of the body before each jump obviously has the function of picking up the sun's position. While the rotation is maximum one turn in sunny weather, animals often need to rotate several times when the sun is not directly visible, e.g. in shadow or after sunset. An ability to identify polarized light may explain the orientation ability under these conditions but may even represent the mechanism under all conditions. Furthermore, several observations may indicate the presence of an "inner clock", which can corrugate for the sun's movement.

The animals were able to keep a constant direction through patches of sun and shade, as well as through open fields and dense forest (Fig. 6). The ability to avoid dark obstacles and resume the original direction (Fig. 2) ensures that long-distance migration is consequent. If the original direction could not be remembered, the frequent confrontation with tree stems could easily result in a meaningless random migration within a restricted area. Because these collembolans are easily trapped in snow depressions (like animal footprints), it is important for them to avoid the funnel-formed snow depressions closely around the tree stems. With ten days of favourable weather during the winter, the present observations indicate that a given population should be able to migrate 2–3 km.

It is not known why different populations have different directions within the same forest. One possibility is that migration starts towards the most open and enlightened part of the environment. Then at least the start of the migration would be on a rather smooth surface with few obstacles. Different directions between, and also within populations probably ensures a genetical mixing, and also that at least certain animals will reach favourable new sites.

#### 4.3. Comparison with strategies of other "snow insects"

*Chionea* sp. (Diptera) and *Boreus* sp. (Mecoptera) are two wingless insects which are often observed on snow in boreal coniferous forests. The animals migrate from the sub-nivean air space along channels created by trees and bushes, and copulate on the snow surface (Strübing 1958). The function of their winter activity is clearly to allow the sexes to meet. *Chionea* has the lowest abundance of the two and is therefore the most active migrator on the snow (Hågvar 1971). Both *Chionea* and *Boreus* are too large to escape vertically into the snow pores when temperature falls. Therefore, they cannot develop a long-range migration strategy, and should not move outside a forest area.

*Chionea araneoides* Dalm. has its greatest abundance on snow at temperatures around  $-4^{\circ}\text{C}$  (Hågvar 1971), occurs mainly in the first half of the winter and lays eggs during mid-winter (Hågvar 1976). *Boreus* sp. occurs on snow at temperatures above zero, mostly near the end of the winter. Egg-laying probably occurs in spring (Hågvar, unpubl.). *Hypogastrura*, *Chionea* and *Boreus* illustrate three different strategies of winter activity, each species taking favour of the snow cover in different ways.

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